

COMMENTARY

“Commentary” is a new section of *Quaest. Ent.* that will appear from time to time, and will contain expressions of opinions about general items, controversial or otherwise, that ought to be of interest to many of our readers. These contributions will not be refereed because they are intended to be free expressions of opinion. Changes by the Editor might be made to the form of presentation, but not to its substance. Remarks that are deliberately abusive or insulting will not be published. Rebuttals to previously expressed views will be considered, but the journal is under no obligation to publish them.

The paper inaugurating “Commentary” addresses an issue that is becoming controversial in cladistic systematics. The author is a distinguished Norwegian dipterist, known principally for his extensive work on and publications about chironomid flies.

The Editor

ON THE LIMITATIONS OF PARSIMONY IN PHYLOGENETIC ANALYSIS

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All sciences unselfconsciously use parsimony as a criterion of hypothesis choice, *i.e.*, as a way of measuring support of alternative hypotheses against a body of evidence. In phylogenetic reasoning “parsimony interprets synapomorphy as evidence for phylogenetic relationship, but denies that symplesiomorphy has this significance” (Sober, 1986:28). Parsimony, however, (again citing Sober) does not itself suffice to solve the problem of incongruent data; character weighting must play an indispensable role. “Parsimony is not a device that tells biologists how to weigh characters; rather parsimony requires that the characters already should be weighted.” Parsimony, however, also enters into the process of character weighting. And character weighting carries with it substantive assumptions about the evolutionary processes.

The question is, then, will the use of parsimony in choosing among alternative hypotheses of explanations of single character distributions, lead to unparsimonious

results when reconstructing genealogy according to the methods of quantitative phyletics and transformed cladism? My contention is that it will. To show this was the main aim of my recent papers (Saether 1983, 1986) and not, as Farris (1986) maintains, to "bolster a contention that postulated homologies can be used as evidence on phylogenetic relationships." I believe that when the monophyly of different groups has been established by "true" synapomorphies, an underlying synapomorphy, but only when appearing as a unique inside parallelism (Brundin 1976) showing principal deviation, may assert monophyly for a collective taxon. Whether or not underlying synapomorphies are operationally recognizable is beside the point, which is that they occur and apparently commonly.

There are four main categories of explanations for the distribution of alternative character transformations of an apomorphic trend within a monophyletic group (Saether 1983). The apomorphy may be explained as: (1), uniquely derived, an "objective" synapomorphy; (2), as caused by parallel selection or convergence (both giving the same distribution of character alternatives); (3), secondary reduction, reversal or change; or (4), underlying synapomorphy *i.e.*, inherited factors causing incomplete synapomorphy. I agree fully with Farris (1986:15) in summarizing parsimony. Genealogical hypotheses are indeed "potentially able to explain observed points of similarity among organisms as the result of inheritance from a common ancestor." "An observation is said to provide evidence favoring a first hypothesis over a second when the first is better able to explain the observation." "A genealogy that is consistent with a single origin of some trait is able to account for all similarities in that trait as inheritance." "Each additional requirement for a separate origin of a feature reduces the explanatory power of a theory of phylogenetic relationship."

To find the hypothesis best able to explain the observed similarities, then, it is necessary to minimize the requirements for independent origins, the most parsimonious explanation for the distribution of alternative character transformations. I have shown (Saether, 1983) that for very many types of character distributions underlying synapomorphy is the most parsimonious solution, and except for uniquely derived "objective" synapomorphy, it always is as good as any alternative explanation. The more times the apomorphic alternative appears separately in the different branches of a monophyletic group, the more all other explanations require additional separate origins, while underlying synapomorphy still is able to account for all similarities in the trait as inheritance with a single origin.

Farris (1986) rejects underlying synapomorphies since they lead to unparsimonious results *in his method* of reconstructing phylogeny. One of my objections to neocladistic methods is that they disregard the most parsimonious explanations of character distributions. I agree with Farris (1985:196) that "any theory that implies both parsimony and a non-parsimonious method must be self-contradictory." In a qualitative method all characters, including underlying

synapomorphy, can be properly judged and weighted in such a way that the search for sister groups can continue in a parsimonious manner. Farris (1986) refers to me as claiming that in quantitative phyletics “the most parsimonious tree is taken as the truth”. I stated that there is no biological evidence that minimum length trees are most in accordance with the “tree”. If Farris is not interested in finding the genealogical hypothesis most likely to be in accordance with the “true” tree, we have different purposes in erecting synapomorphy diagrams.

If underlying synapomorphy always is at least as good an explanation as parallel selection or secondary change why is it not used as the prime explanation? Farris touches on this in his contention that I omit an explanation for underlying synapomorphy. An explanation of the possible mechanisms is given in Saether (1983). The potential information classes of Wiley and Brooks (1982:4) are descriptions of underlying synapomorphy. However, the mechanisms in question apparently cause the expression or non-expression to function like an on-off switch. There seldom are intermediates. Nonetheless, secondary reduction and parallel selection often can be followed through several steps often corresponding with environmental changes and obvious functional adaptations. Usually, they are easy to spot, with sufficient knowledge of the group studied. Knowledge and judgment, or what Humphries and Camus (1986:95) label intuition, are alternative necessary elements in choosing between hypotheses of character distribution. To repeat the citation from Hennig (1966:120) given in my paper: “Characters cannot be considered in isolation, even in regard to transformation series of other characters.”

According to Farris, one of the main grounds offered by me for using homoiology should be that Hennig recommended it. I stated that Hennig in his theoretical works did not recommend it. Hennig (1966), as also stated by Farris, dismissed parallelism as equivalent to convergence for purposes of phylogenetic analysis, as he dismissed multiple derivations. In his practical work, however, he used both. In the citation by Farris, Hennig (1966:121) discussed the interpretation of character distributions. The first alternative for choosing between two contradictory characters with respect to phylogenetic relations is that “(1) It was erroneous to interpret one or both characters as plesiomorphous or apomorphous”; *i.e.*, they are not synapomorphous. Multiple derivations of a synapomorphy thus are included in (2) parallelism. Yet, as shown by me and repeated by Farris, Hennig, in actual practice, used underlying synapomorphies as if they were “true” synapomorphies.

The first paper in which I used the term underlying synapomorphy (Saether, 1977) was refereed by Hennig. He did not raise any objection to the term. Schlee was a pupil and close collaborator of Hennig. His opinions of Hennig’s theoretical viewpoints therefore carry particular weight. While Schlee (1968) in his excellent revision of the *Corynoneura*-group follows Hennig’s practical applications, in his paper of 1971 and particularly 1975 (a) he noted the consequence of Hennig’s theoretical writings. Here, Schlee recognizes uniquely derived synapomorphies, *i.e.*,

“objective” synapomorphies, as the only basis for reconstructing genealogy since all other alternatives, including subjective synapomorphy, would cause loss of explanatory power in the reconstructed genealogy. He is strongly critical of Brundin (1966) as well as of his own work from 1968. That Farris finds Schlee’s paper unobjectionable and undogmatic is a result of reference to the wrong paper. (Schlee, [1975 b] a critique of numerical phyletics.) It is, however, clear that if using the criteria of Schlee for asserting synapomorphy, *i.e.*, using “objective” synapomorphy only, both neocladistic methods and transformed cladism would be workable, but superfluous.

A complete set of “objective” synapomorphies, is, by definition, the “true” phylogenetic tree and is easily transformed into a dichotomous diagram without the help of calculators or computers (Schlee 1975 b). The number of “objective” synapomorphies, however, usually is sufficiently large only when comparing higher taxa (Saether 1986). Clique methods, transformed cladism, and dogmatic cladism all either recognize “objective” synapomorphy, only, or give such features nearly exclusive weight. It is thus not a deception, as maintained by Farris, to state that the same critique is valid against all of those three systems of analysis even when the exponents of each object to the other’s methods.

Farris, in his chapter on homoiology includes parallelism (*i.e.*, parallel selection, homoiology and, by implication, multiple derivations) with convergence in homoplasy. He equates homoplasy with nonhomology, as is common practice. As shown by Saether (1983), if characters are defined as including different character states, parallel selection will be included in definitions of homoplasy, but not in nonhomology. Underlying synapomorphies are homologies, the common character consisting in the common capacities to develop the same feature. They can be regarded both as homoplasious or as non-homoplasious depending on whether the character itself or the capacity to develop the character is considered. When I maintained that homoplasy is “nearly universal” I was referring to the wider meaning of homoplasy as used by Farris. When homoplasy is involved in 275 of 291 trends (Saether 1986, table 1), and only two of the 291 trends are “objective” synapomorphies showing principal deviations, homoplasy must be regarded as “nearly universal”. This also clearly demonstrates the need for using all available characters in estimating genealogy. If Farris dismisses the “necessity argument” (Farris 1986:16) why does he recommend the use of characters showing outside parallelism, *i.e.*, multiple derivations?

It is of little importance whether one of the methods of Felsenstein, Estabrook or Farris are better than the other for estimating genealogy. My intention was to show that while they all are quantitative methods and fail to take all types of characters into account, they lead to different results and are based on different philosophies. (I did not, as stated by Farris, cite Patton and Avis (1983), but Dupuis (1984) as advocating qualitative over quantitative techniques.)

Quantitative phyletics, however, is well-suited for estimation of anagenetic levels (Saether 1979). Farris significantly neglects to address the important distinction between cladogenetic and anagenetic trends and analyses. Cladogenetic analysis should be qualitative, while anagenetic analyses are quantitative. The search for sister groups, *i.e.*, cladogenetic analysis, involves choosing theoretical ancestors for later species. Starting with the lowest taxa, for instance species, to be included in the analysis the scheme of argumentation is gradually built up to include more inclusive groups. It is what Sober (1986) calls thinking backward. In order to include a species in a synapomorphy diagram, it is in principle sufficient to know that one single character it shares with its sister species is uniquely derived.

Anagenetic analysis, on the other hand, evaluates the attributes of the theoretical progenitor of the monophyletic group under study and estimates deviations from the ancestor in its proposed descendants. In principle, to find the correct anagenetic levels for all included taxa, every single trend evaluated needs to be scored as apomorphic or plesiomorphic relative to the progenitor. This is what Sober calls forward thinking. The difference in treatment will be clear for instance from Saether (1976) which forms the base for table 1 in Saether (1986). It can be noted that underlying synapomorphies were not used as evidence of phylogenetic relationships. In the synapomorphy diagrams forming the base for tables 2 and 3 (Saether, 1986) only a few underlying synapomorphies showing unique inside parallelism of principal deviations were used.

There is nothing wrong with *a posteriori* postulation of natural processes from patterns in the distribution of characters, testing these patterns in other schemes of argumentation, and then using the theories in the building of genealogical hypotheses. As stated by Ridley (1986), the argument proceeds not in a circle, but by "successive approximation". The sequence – hypothesis, test, further hypothesis – is not circular. The chain of inductive-deductive or hypothetico-deductive reasoning is a common scientific method. What transformed cladists, numerical taxonomists, and, apparently Farris, object to is not circular reasoning, but theoretical ideas. Theories, in science, if they are interesting, are always taken beyond evidence, and assumed in further tests (Ridley [1986]). Hennig, as shown by the last citation in my paper, recommended that this be done.

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